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Species richness and the level of knowledge of the bryozoan fauna of the Arctic region

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ABSTRACT

The publication presents the results of the analysis of retrospective data and samples of bryozoans collected in different seas and areas of the Arctic region during recent 30 years. To date, 518 species of bryozoans have been recorded in the Arctic, which is on 26.4% more than previously registered. The level of increase in species numbers in the species lists of the regional faunas was different in different areas. In the waters of Greenland, the found species diversity of bryozoans was on 12% higher; in the Barents and Kara Seas – on 18 and 19%, respectively; in the Laptev and East Siberian seas – on 30%; in the Faroe Islands waters on 30% than it was previously marked. In the Icelandic waters and the Chukchi Sea, the number of bryozoan species is richer by five and two times respectively than it was considered earlier. Our assessment of the modern knowledge of the fauna of this group using the method of rarefaction showed that the bryozoan fauna is still underexplored. The Chao metric calculations also indicate that expected species richness would increase by 10–30% in different areas of the Arctic in case of additional sampling efforts. At the same time, a measure of taxonomic distinguish of the fauna allows to conclude that the species composition of bryozoans has already been sufficiently studied in most of the considered areas of the Arctic zone except in the waters of the Canadian Arctic Archipelago.

Key words: Arctic, bryozoans, species richness, state of knowledge

Видовое богатство и степень изученности фауны мшанок Арктического региона

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РЕЗЮМЕ

В работе представлены результаты анализа ретроспективных данных и проб мшанок, собранных в разных морях и районах Арктического региона за последние 30 лет. На настоящий момент там зарегистрировано 518 видов, что на 26.4% превышает ранее известные сведения о видовом богатстве этой группы. Отмеченное увеличение числа видов было неоднозначным в разных районах Арктики. По сравнению с более ранними сведениями разнообразие фауны мшанок в водах Гренландии оказалось выше на 12%; в Баренцевом и Карском морях на 18 и 19% соответственно; в Лаптевых и Восточно-Сибирском морях – на 30% в каждом, а в районе Фарерских Островов на 30%, а в Чукотском море и в водах Исландии – в 2 и в 5 раз выше прежнего. Вместе с тем, проведённая оценка изученности фауны этой группы с использованием метода разрежения Уорвика – Кларка показала, что фауна мшанок остается все еще недоизученной. На это указывают и результаты вычислений метрики Чао, согласно которым, при дальнейших исследованиях, возможно увеличение видового богатства мшанок еще на 10–30% в разных районах Арктики. В то же время, оценка таксономической выраженности фаун позволяет заключить, что видовой состав мшанок в большинстве рассмотренных районов Арктической зоны изучен вполне удовлетворительно, за исключением вод Канадского Арктического Архипелага.

Ключевые слова: Арктика, мшанки, видовое богатство, изученность

INTRODUCTION

The first most notable synopsis on the Arctic bryozoan fauna was the work by R. Osburn (1919). In addition to his own observations, the author compiled the information concerning the bryozoan fauna in the Greenland waters published by 12 other researchers from the late eighteenth to the early twentieth century (Fabricius 1780; Smitt 1879; Kirchenpauer 1874; Lütken 1875; Busk 1881; Hennig 1896; VanHoffen 1897; Andersson 1902; Bidenkap 1905; Norman 1906; Kluge 1907; Levinsen 1916). For this area, Osburn (1919) listed 178 bryozoan species and noted that the diversity of the bryozoan fauna is higher here than in the other parts of the Arctic.

The most important milestone in providing a generalization of the previous data on the Arctic bryozoans was a monograph and identification guide "Bryozoans of the northern seas of the USSR" by G.A. Kluge (1962). In this monograph, G.A. Kluge has summarized a voluminous body of literature pertaining to the study of bryozoans in the Arctic seas (e.g., Smitt 1868a, b, 1871, 1878; Urban 1880; Vergelius 1884; Nordgaard 1918, 1923, 1929; Bidenkap 1900, Anderson 1902, Norman 1903a, b; Waters 1900) including the results of his own observations (Kluge in Derjugin 1915; Kluge 1929; Kluge in Gorbunov 1946; Kluge in Ushakov 1952; ect.).

Kluge's monograph presented detailed information on distribution of bryozoan species not only the Arctic seas, but also on their records outside the Arctic region. The information was supplemented by the data on depths, temperature and substrates, on which particular species were found. G.A. Kluge was the first to provide the most complete species list of bryozoans known at that time from the seas of the Eurasian sector of Arctic, with additional information on their occurrence in Western Arctic. Altogether, the monograph included the information on 341 species of the Bryozoa (Kluge 1962).

In 1954–1957 and 1958–1959, several large-scale benthic surveys were conducted in the south-eastern part of the Barents Sea (Pergament 1957; Gostilovskaya 1976, 1984) and in the Greenland Sea (1956) (Koltun 1964). The new information gained from these surveys has expanded our understanding of species richness and distribution of bryozoans in the Arctic seas, but the faunal synopses for the Arctic region still used the information from Kluge's (1962) monograph until the end of the 1980s (Gontar and Denisenko 1989).

In contrast to the bryozoan fauna of Greenland and Russian Arctic seas, which had already been more or less thoroughly studied, the information on bryozoans from Iceland, Faroes Islands and Canadian Arctic Archipelago remained scarce and fragmentary up to the end of the 20th century (Kramp 1934; Hincks 1877; Nordgaard 1924; Powell 1968, etc.).

In the second half of the 20th century and the early 2000s, numerous expeditions to the continental shelf and the upper bathyal of seas and the areas of the Arctic region provided a powerful impetus for renewal of the study of the Arctic bryozoan fauna. This process was accompanied by an increased intensity of exploration, because the samples were collected sequentially, along a relatively regular grid of stations, which encompassed large areas in different regions of the Arctic.

These expeditions provided the abundant new material on the bryozoan fauna, which allowed an estimation of the bryozoan species richness in those regions that had previously been little studied or completely unexplored.

The results of the analysis of these newly collected materials have partly been published. But it was mostly faunistic reviews or species lists with notification on new records of bryozoans in regional faunas of the Arctic, while the detailed descriptions and assessments of species richness were in most cases lacking (Gontar 1990, 1994, 2001, 2004; Brattegard 1997; Palerud et al. 2004; Denisenko 2008, 2009a, 2011; Denisenko and Kuklinski 2008; Denisenko et al. 2016; etc.). At the same time, the examination of the bryozoan samples collected during the expeditions using scanning electron microscopy has led to the discovery and description of species new to science in different seas of the Arctic region (e.g.: Hayward 1994; Gontar 1996; Kuklinski and Hayward 2004; Kuklinski and Taylor 2006, 2008; Kluge 2009; Denisenko 2009b, 2015, 2016a, b, 2018a, b). New data on distribution of known species of this group in the seas of the Arctic region and outside the Arctic have changed the prevailing opinion on the biogeographical status of some species (Denisenko 2008, 2010; Denisenko et al. 2016).

In recent decades, the studies of bryozoans have been conducted using statistical methods to estimate the correlation between the diversity of the group and the environmental factors, but this analysis has so far been made only for some of the Arctic areas (Denisenko 1990, 1996, 2001, 2010, 2017; Denisenko and Grebmeier 2015; Denisenko et al. 2016).

At the same time, despite all the aforementioned studies, some information remains unpublished and there is still no estimate available for the status of knowledge regarding the bryozoan species richness in the Arctic seas. The need for such estimate is crucial, because there has been an increasing number of reports on the occurrence of alien species in different areas of the World Ocean, although the degree of their non-nativeness can be reliably estimated only if the native fauna of these areas is sufficiently well known.

The aim of this study was to estimate the current level of knowledge concerning the bryozoan fauna and to estimate the expected number of bryozoan species in the regional faunas of the Arctic region.

MATERIAL AND METHODS

A definition of ‘Arctic region boundaries’ was accepted on base of a schemes proposed by Hydrography Service of Russia (Gorshkov 1980) with additions suggested by CAFF, the Conservation of the Arctic Flora and Fauna working group of the Arctic Council (Vongraven et al. 2009). The CAFF boundary of the Arctic in the Northern Atlantic extends down to the Faroe Archipelago, Iceland, through the Norwegian and into the Northern Seas. In the Pacific sector, the Arctic boundary corresponds to the Bering Strait separating the Chukchi and Bering Seas (Gorshkov 1980).

The present study includes the results of analysis of the taxonomic collections and catalogues of the ZIN RAS, personal collections of the author as well as the samples collected by colleagues at the ZIN, PINRO and MMBI. The recent bryozoan samples were also collected during the expeditions carried out as part of international programs (Russian–Norwegian Programs “CABANERA” and “BASICC”, Russian–American Program “RUSALCA” and Russian–German Program “Laptev Sea Ecosystem”) in 1993–2012. The sampling area encompassed the Russian Arctic seas (Barents, Kara, Laptev, East Siberian and Chukchi Seas). The study also used the material of historical and recent samples collected in the waters of Iceland, Greenland and the Faroe Islands. The materials are stored in the Museum of the University of Tromsø, the Natural History Museum of Denmark (Copenhagen), the Natural History Museum of the Faroe Islands (Kaldbak), the Icelandic Institute of Natural History (Reykjavik), and the Greenland Institute of Natural Resources (Nuuk).

In total, about 3500 samples were examined, which were collected from more than 2600 stations (Table 1), and more than 20000 taxonomic identifications of bryozoans were performed.

The current status of knowledge of the fauna was analyzed using the Sanders rarefaction method (Sanders 1968) that provides a graphical estimation, by plotting the cumulative curves, for the extent to which the bryozoan fauna has been studied. The values for the plots were obtained through numerous permutations of per-station values of species numbers recorded for each station in each of the studied areas (Clarke and Warwick 1994).

The expected species richness was estimated with the *Chao2* metric (Chao 1989) using the following formula:

$$S_{chao} = S_{obs} + \frac{(m-1)}{m} \cdot \frac{Q_1(Q-1)}{2(Q+1)}$$

where S_{obs} is the total number of species observed in the regional fauna, m is the number of the samples analyzed, Q_1 is the number of species observed in a single sample and Q is the number of the recurrent species that occur at least in two samples.

The complexity of the taxonomic structure of the bryozoan faunas in the study areas was estimated using the taxonomic diversity index calculated for the “presence/absence of species” (Clarke and Warwick 1998; Maggurran 2004; Hammer 2019).

The statistical analysis and data processing were performed using the Excel, Statistica (version 8), Primer (version 5), and PAST (version 3.26) software packages.

Table 1. Number of analyzed stations in the studied areas of the Arctic region.

Areas	Number of stations
Barents Sea	809
Kara Sea	332
Laptev Sea	177
East Siberian Sea	95
Chukchi Sea	128
Canadian Arctic Archipelago	129
Greenland waters	314
Icelandic waters	295
Faroe Archipelago waters	364
Totally:	2643

RESULTS

The analysis of all available literature, taxonomic catalogues and the results of the taxonomic identification in new samples shows that the species list of bryozoans in the Arctic now includes 518 species. The analysis of all evidence suggests that the richness of regional bryozoan faunas is currently significantly different in various Arctic areas (Table 2). The most diverse fauna of bryozoans was found in the waters near Greenland and Iceland (western sector of the Arctic) and in the Barents Sea (eastern sector). In the Chukchi and Kara Seas, and in the waters of the Faroes Islands, the number of species was somewhat lower than in the aforementioned areas. The poorest bryozoan fauna was noted for the Laptev and East Siberian seas and for the Canadian Arctic Archipelago.

The use of the *Chao2* metric (Chao 1989) shows that the number of species in the species list can increase by 10–30% in different areas of the Arctic region (Table 2).

The analysis of the current status of knowledge of the bryozoan species richness using the Sanders rarefaction method (Clarke and Warwick 1994) demonstrates that in most cases the shape of the rarefaction curves obtained through permutation of the per-station data does not reach the asymptote (Fig. 1). These results, together with the calculation of the Chao2 metric (Chao 1989), show that registered species numbers for the regional bryozoan faunas cannot be regarded as final values.

The taxonomic complexity (distinguish) index of the regional bryozoan faunas in the Arctic (Δ) has demonstrated that the values of this parameter are significant in all Arctic areas excluding the Canadian Arctic Archipelago where the values were outside the significant rate ($p > 0.05$). This can be taken as evidence of a taxonomically simpler structure of the bryozoan fauna in the latter region (Table 3).

DISCUSSION

The number of species of bryozoans registered in the Arctic region (518 species) at present time is one-third (33.7%) higher than in the species list previously provided by Kluge (1962) for the Arctic region. The registered number of bryozoans is more than one-fourth (26.5%) as high as the number that it has been indicated for this region at the end of the 2000s (Josefson et al. 2013).

Table 2. Observed and expected species richness of the bryozoan fauna in the different areas of the Arctic region estimated on *Chao2* metric (Chao 1989).

Area	Bryozoan species number found at present	Expected species richness
Barents Sea	328	349 ± 10
Kara Sea	226	258 ± 18
Laptev Sea	178	210 ± 15
East Siberian Sea	137	157 ± 15
Chukchi Sea	219	255 ± 18
Canadian Arctic Archipelago	98	158 ± 5
Icelandic waters	307	335 ± 18
Faroes Archipelago waters	232	236 ± 14
Greenland waters	309	369 ± 19

Table 3. Taxonomic distinguish (Δ) in the regional bryozoan faunas of the Arctic region.

Area	Taxonomic distinguish (Δ)	95% lower confidence range of Δ	95% upper confidence range of Δ
Canadian Arctic Archipelago	**3.187**	**3.227**	3.42
Greenland waters	3.33	3.263	3.377
Icelandic waters	3.297	3.256	3.384
Faroe Archipelago waters	3.283	3.25	3.393
Barents Sea	3.37	3.26	3.379
Kara Sea	3.381	3.247	3.392
Laptev Sea	3.374	3.238	3.403
East Siberian Sea	3.342	3.232	3.405
Chukchi Sea	3.288	3.248	3.389

As mentioned above, a significant increase in species list number was caused not only by the description in the Arctic of 30 species new to science over the course of the last 30 years (Hayward 1994; Gontar 1996; Kuklinski and Hayward 2004; Kluge 2009; Kuklinski and Taylor 2006, 2009; Denisenko, 2009, 2015, 2016a, b, 2018a, b, etc.). It was also a consequence of the records of the species previously unknown for the Arctic and found in different subpolar regions during the period from 1992 to 2016 (Denisenko 1990, 1996, 2000, 2010, 2011; Gontar 1994, 2001, 2004; Denisenko and Kuklinski 2008; Denisenko et al. 2016).

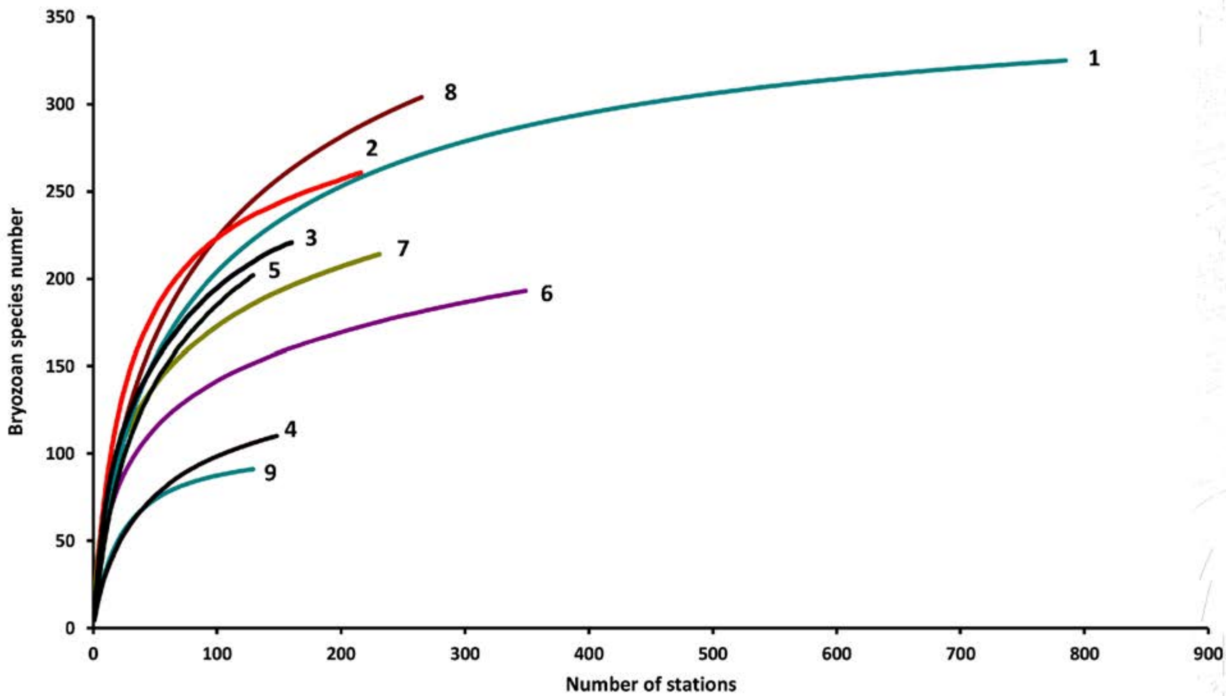


Fig. 1. Station-based rarefaction curves (average curves from 900 permutations) of bryozoan species increase for Arctic shelf area. 1 – Barents Sea; 2 – Kara Sea; 3 – Laptev Sea; 4 – East Siberian Sea; 5 – Chukchi Sea; 6 – Faroe Archipelago; 7 – Iceland; 8 – Greenland; 9 – Canadian Arctic Archipelago.

The conclusion that bryozoans in the Arctic region are one of the most species rich groups of benthic invertebrates was made already in the early 2000s (Sirenko 2001) based on the studies conducted before the mid-twentieth century (Kluge 1962; Gontar 2001). Further accumulation of information on the bryozoan fauna has confirmed their dominant status in terms of number of species compared to many other taxonomic groups. It has been established that the bryozoans in various areas and seas of the Arctic region are surpassed in species richness only by polychaetes, crustaceans and molluscs, and in the Chukchi Sea they exceed all other major taxa in species numbers (Denisenko 2017; Jorgensen et al. 2017).

As mentioned above, the extend of the species list for the bryozoans of the regional Arctic faunas was the consequence of the integration of the data contained in the taxonomic catalogues and the results of taxonomic identification of the zoobenthic samples collected in recent years, with consideration of the previously published information. The level of increase in species numbers in the species lists of the regional faunas was different in different regions. In the best-studied areas, such as the Barents and Kara seas and the waters around Greenland, the increase in species numbers was minimal (18, 19 and 12%, respectively). In the Laptev and East Siberian seas, the number of reported species has grown by one third (Gontar 2004, with our additions; Denisenko 2010, 2011), and in the Chukchi Sea this number has increased nearly twice (Denisenko 2008, 2009a; Denisenko and Grebmeier 2015). (Table 2). Exclusively new records and descriptions of new species (Denisenko 1990, 1996, 2000, 2008, 2010; Gontar 2001, 2004; Denisenko et al. 2016) caused the marked increase in species numbers in the Russian Arctic seas. In contrast, in the Chukchi Sea, the increase was due to the integration of the data on the bryozoan fauna from its western part (Kluge 1962), which is under the Russian jurisdiction, with the data on the species composition of bryozoans inhabiting the eastern part of the sea, which is under the American jurisdiction (Osburn 1955; Feder and Jevett 1978).

An increase in intensity of benthic studies in the 1980–1990s in the areas around Iceland and the Faroes Islands was a major reason for the change in understanding of the richness of the bryozoan fauna in these areas of the Arctic. The combination of the newly collected data with the information from catalogues of the Natural History Museum of Denmark, which relied on collections from the beginning of the twentieth century (Hansen, personal communication), allowed us to increase the number of bryozoan species considerably. As a result, the species list of bryozoans from the Icelandic waters increased almost five times compared to the previously known data from literature (Hincks 1877; Nordgaard 1924; Kluge 1962; Bryazgin et al. 1981; Stępień et al. 2017). For the continental shelf and upper slope of the Faroe Islands and adjacent shallow-water areas of the Atlantic Ocean, the observed species richness of bryozoans has increased almost on 1/3 (Denisenko et al. 2016) compared to the previous information contained in scattered publications (Hasenbank 1932; Kramp 1934; Jensen and Fredriksen 1992; Hayward 1994; Klitgaard 1995; Dinesen 1996; Hayward and Ryland 1996; Hansson 1999).

After the analysis of the material collected in the course of several expeditions of the 1990s, the observed species richness of bryozoans in the Siberian seas has also changed significantly. However, it is still 1.5–2 times as low as in the Barents Sea or in the waters of Greenland and Iceland. The lack of recent studies on the bryozoan fauna from the Canadian Arctic Archipelago is the reason for a relatively short list of bryozoan species in this region, where the apparent number of species is three times as low as in the waters near Greenland. The relative poorness of the fauna in the Siberian seas and the Canadian Arctic is primarily associated with the absence of bryozoan species – typical inhabitants of temperate latitudes that penetrate into the Arctic with the Atlantic and Pacific waters – and also with the lack of relatively widely distributed species of the Atlantic or Pacific origin.

The systematic studies spanning several decades have addressed, to some extent, the paucity of information on species richness of the bryozoan fauna in the Arctic region. However, the question as to how well the fauna of this group has been studied in the Arctic remains unanswered. This kind of information is particularly important, because, as mentioned above, the fundamental understanding of the background status of biota would allow a more accurate estimation of possible changes in biodiversity under the influence of natural and anthropogenic factors and would permit an identification of invasive alien species.

There are several methods currently in use that provide estimators for species richness (Gray et al. 1997; Gray 2000, 2002). The use of these methods, however, produces some discrepancy in the final results. This discrepancy can be explained by the aforementioned irregular arrangement of sampling stations and by an insufficient density of the grid of sampled stations in different aquatic areas in combination with a non-uniform distribution of species within these areas.

A commonly applied method of estimating the species richness is the use of asymptotic models. This technique has often been criticised, because the plots almost never reach the plateau (Pesenko 1982; Clarke and Warwick 2001; Denisenko 2013). However, the present study employed the mathematical algorithms, which are part of the most widely used computer programs designed to estimate the current status of knowledge of species richness in regional faunas (Clarke and Warwick 2001; software). In particular, we used the rarefaction method (Sanders 1968; Clarke and Warwick 1994), which, despite the criticism from some authors (Gray 2000), has been applied by a number of hydrobiologists for the estimation of the level of knowledge of the faunas (e.g., Piepenburg et al. 2011; Denisenko 2013). The application of this method enables a comparison between our results on bryozoans and the results of similar analyses on other groups of marine invertebrates.

The rarefactional (permutational) data calculated in the present study for various areas of the Arctic reflected different intensities, with which the observed species grew in number with an increasing number of stations. The number of stations, where the bryozoans were collected, varied greatly across the seas (Table 1), and the steepness of the curves, which is an indirect measure of the diversity of biotopes, was also different, but none of the curves approached the asymptote. The shape of the curves can also be regarded as an indirect indicator of the diversity of bottom sediments and substrates in the study area. The curve, which was the closest to the asymptote, reflected a growing number of bryozoan taxa with an increase in sampling efforts in the Barents Sea, where these animals were collected from more than

750 stations. The results of the analysis, however, suggest that the species richness of bryozoans to be expected in the Arctic seas must be even higher than that reported in the present study. Furthermore, all the above evidence indicates that the bryozoan fauna of the Arctic region still remains substantially underexplored. On the other hand, since the cumulative increase in species numbers in each successive sample changes in a different manner in each of the study areas, the shapes of the curves obtained for each sea or region indicate that in planning new studies a more complete exploration of the regional faunas would require different intensity of study efforts in different regions of the Arctic. Judging from the shape of the curves, it can be concluded that less effort would be required to complete the study of regional bryozoan faunas in areas such as the Canadian Arctic Archipelago, the Kara Sea and the Faroe Islands.

Difficulties associated with determining the actual species richness in the water bodies are well known. As noted above, they are caused primarily by the sporadic nature of the studies conducted in each region and the uneven distribution of stations across the seas.

Our assumption that the bryozoan fauna of the Arctic region is underexplored, which was based on the analysis of permutational cumulative curves, is further confirmed by the results of calculation of the A. Chao's prognostic metric (Chao 1989). This model, which was specifically designed to estimate the value of the expected species richness, yields the expected number of species, and in each of the seas included in the analysis the use of the *Chao2* coefficient predicts a possible increase in species richness by 10–30% if additional samples were collected (Table 3). The exceptions are the faunas of the Barents Sea and Greenland. According to our studies, the number of newly found species in these regions would not exceed 1.5–2.0% of the currently known number of bryozoan species. This result was completely expectable.

Our conclusion that the bryozoan fauna is underexplored is in good agreement with the conclusions made by Piepenburg et al. (2011) from the results of similar studies on other phyla of benthic marine invertebrates such as molluscs, echinoderms and polychaetes, which are better studied than bryozoans.

To ensure a better reliability and validity of the data on species richness of the present Arctic fauna, the characteristic of the fauna known as taxonomic diversity or taxonomic distinctness was used (if the initial data are scored as "absence/presence of species", both indices become identical). This parameter does not depend on the number of sampling efforts (Clarke and Warwick 1998; Maggurran 2004), because, as mentioned above, the accuracy of results of studying the faunal richness if other aforementioned methods were used, can significantly depend on intensity and evenness of distribution of the sampled stations (Clarke and Warwick 1998; Maggurran 2004, our data). The values of taxonomic distinctness can be computed both for quantitative and qualitative data. The latter is quite important in determining the current state of knowledge of the bryozoan fauna, because during many expeditions the use of qualitative tools for collecting the material on bryozoans makes it impossible to obtain the information on the quantitative representation of species of this group. The estimation of the taxonomic complexity of regional bryozoan faunas using the Clarke and Warwick (1998) method, the so-called taxonomic diversity or taxonomic distinctness index, shows (Δ) that the bryozoan fauna in most regions of the Arctic was adequately explored. Unfortunately, the use of the data on the presence/absence of species at the stations does not provide the detailed information on the expected faunal richness. The results, however, are statistically significant, because the values of Δ lie within the 95% confidence interval. The exception is the current level of knowledge of the bryozoan fauna of the Canadian Arctic Archipelago, where the taxonomic index (Δ) is not only lower than in the other areas, but also falls outside the 95% interval. This result gives credence to our assumption that only the fauna of the Canadian Arctic is still insufficiently explored.

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